# Palaeocene wood from the Republic of Mali

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## Synopsis

A new species of fossil Leguminosae, ?*Caesalpinioxylon moragjonesiae*, is described from the Tertiary deposits of the Tilemsi valley area, Republic of Mali. Anatomical comparison is made with Recent and fossil woods. Silicified vestured pits are illustrated for the first time using the scanning electron microscope. It is suggested that more studies of such pits would assist in classification of fossil dicotyledonous wood.

## Introduction

In 1981 a joint British Museum (Natural History)/Kingston Polytechnic expedition visited the Tilemsi valley area of Mali, west Africa. At Samit, specimens of fossil wood were collected from strata of Middle to Upper Palaeocene age (Krasheninnikov & Trofimov 1969; R. T. Moody, personal communication). The object of this paper is to describe the structure of the petrified wood, which represents a new species of fossil Leguminosae. Particular emphasis is placed on study of the vestured vessel pitting.

## Material and methods of study

The three pieces of wood are silicified, the largest measuring some 18 cm by 8 cm. Thin sections were prepared in standard orientations for observation by optical microscopy. Study of the pitting was also made by scanning electron microscopy (SEM), using fractured chips of the wood (Beck *et al.* 1982). The average density of vessels per unit area was determined by counting as an individual any vessel present, whether or not it occurred as a solitary vessel or as one component of a radial multiple (Wheeler 1986). The number of solitary vessels as a percentage of the total was also calculated.

## Systematic description

### Order ROSALES

### Family LEGUMINOSAE

### Organ-genus *CAESALPINIOXYLON* Schenk, 1890

### ?*Caesalpinioxylon moragjonesiae* sp. nov.
#### (Figs 1–25)

DIAGNOSIS. [Secondary xylem known only]. Vessels diffuse porous, 5 per $mm^2$, solitary (54–59%) and in radial multiples of 2–8, tangential diameter means 154–173 $\mu$m, element length means 225–328 $\mu$m, pits bordered and vestured, 4·5–7 $\mu$m diameter. Parenchyma mainly vasicentric with some confluences, also marginal and locally banded, strand parenchyma rare and probably crystalliferous. Rays multiseriate, subhomogeneous to heterogeneous III, with few uniseriates, 1–4 cells wide (range 18–55 $\mu$m) but predominantly 2 cells wide (28–45 $\mu$m), height means 260–300 $\mu$m (11–13 cells). Fibres libriform, thin-walled, rarely locally septate, with very infrequent, indistinctly bordered pits. Traumatic axial canals, in tangential series, usually present.

NAME. In memory of Miss Morag Jones, palaeobotanist, who died during the 1979/80 expedition to Mali.
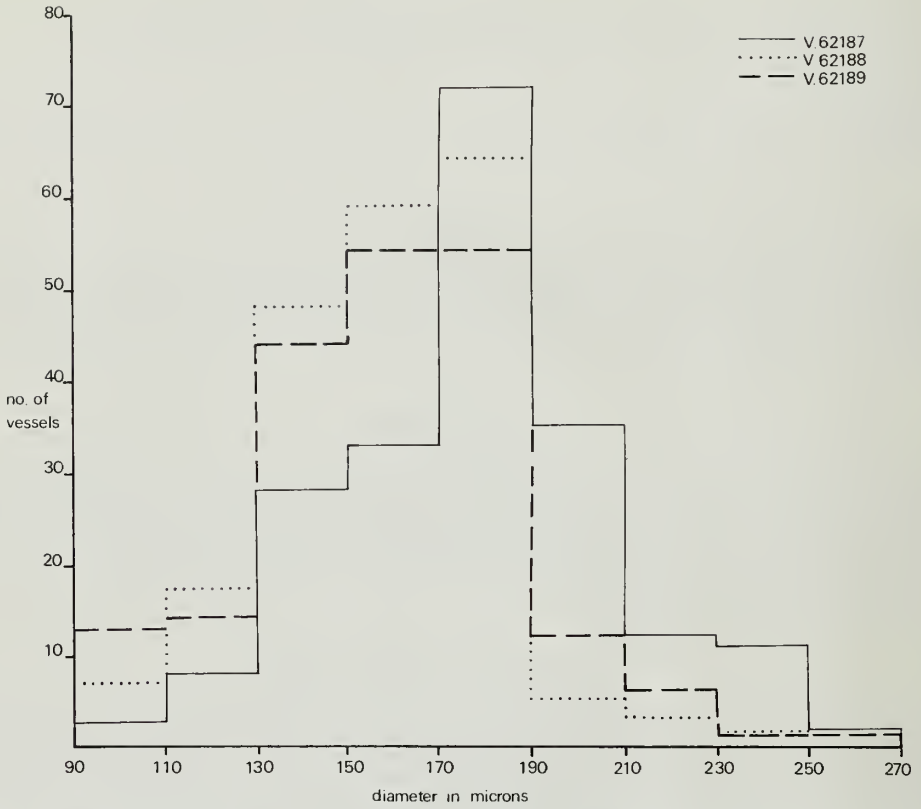
Fig. 1 Vessel tangential diameter in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 vessels measured per specimen).
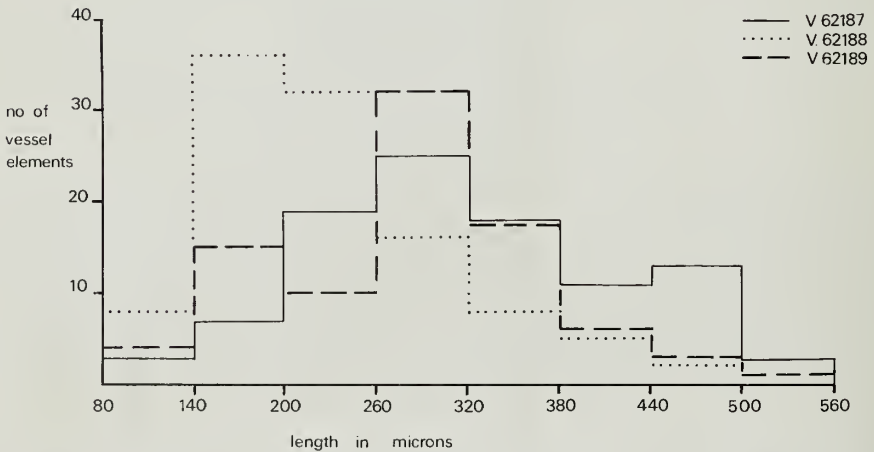


Fig. 2 Vessel element length in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 vessels measured per specimen).
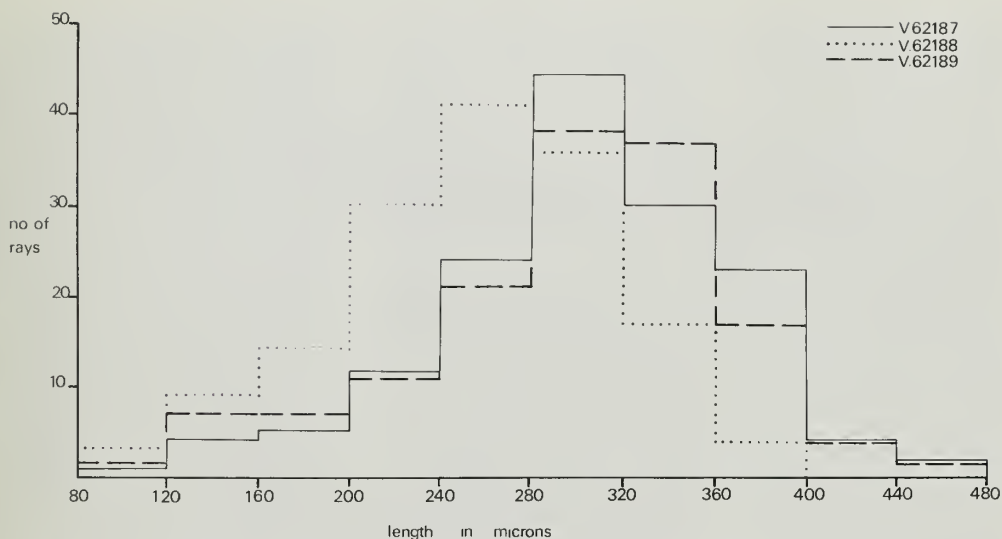
**Fig. 3**   Ray length in *?Caesalpinioxylon moragjonesiae* sp. nov. (100 rays measured per specimen).

HOLOTYPE. BM(NH) V.62187 (plus slides a to l and stubs m, n).

OTHER MATERIAL. V.62188 (plus slides a to j and stubs k, l); V.62189 (plus slides a to c).

LOCALITY AND HORIZON. Limestone and calcareous marl deposits. Middle to Upper Palaeo-
cene; Samit, 100 km NE of Gao, Republic of Mali.

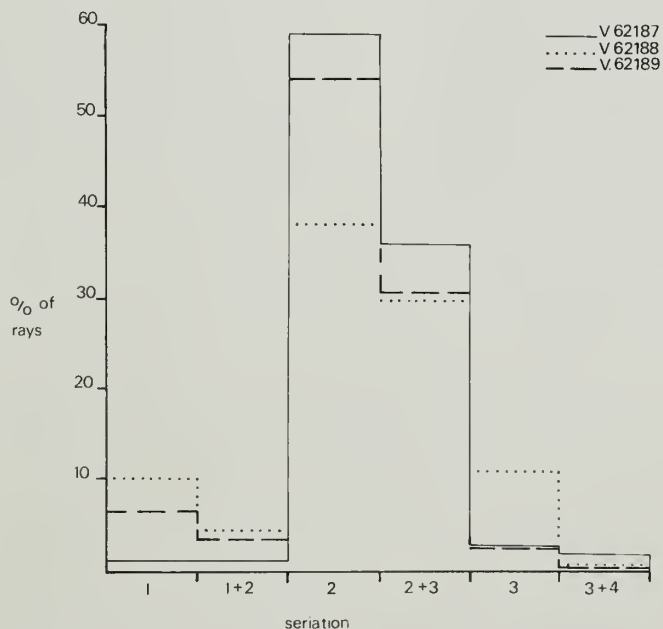DESCRIPTION. *Vessel elements.* Diffuse porous (Fig. 6), solitary 54–59%, remainder in radial



**Fig. 4**   Ray seriation in *?Caesalpinioxylon moragjonesiae* sp. nov. (100 rays per specimen).
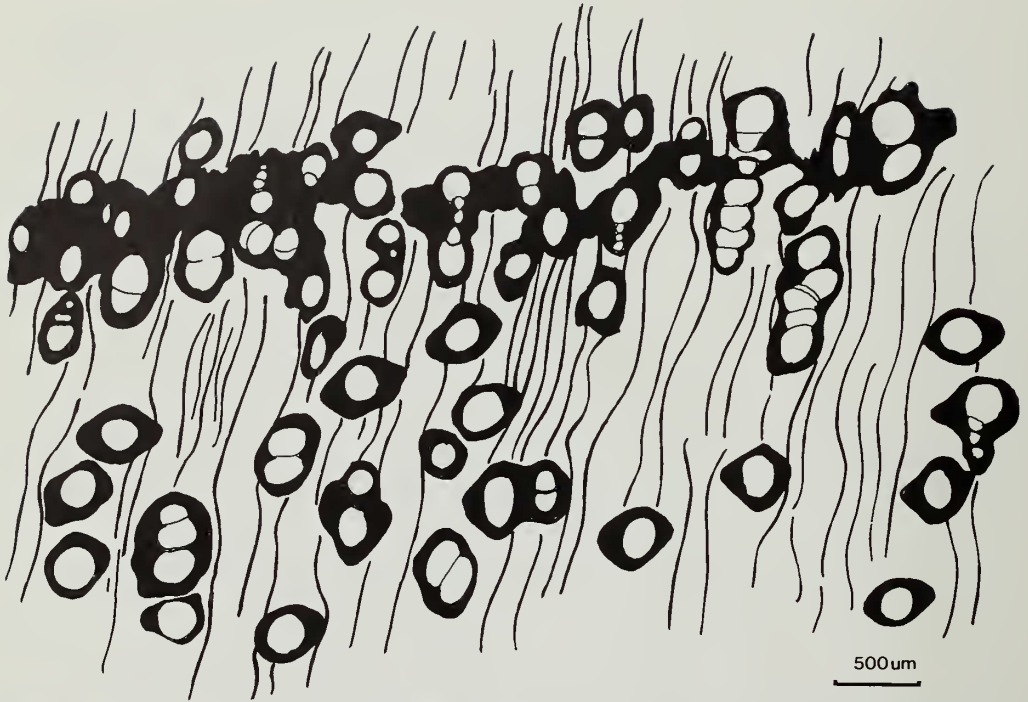
**Fig. 5** Transverse section of *?Caesalpinioxylon moragjonesiae* sp. nov., showing terminal paren-
chyma at top of figure and some paratracheal parenchyma (solid black areas). Sinuous lines show
position of rays. Holotype, V.62187.

multiples of two to eight; tangential diameter 63–252 $\mu$m, mean 154 $\mu$m (V.62189), 156 $\mu$m
(V.62188), 173 $\mu$m (V.62187) (Fig. 1); two to ten per mm$^2$, mean five, length 72–558 $\mu$m, mean
225 $\mu$m (V.62188), 292 $\mu$m (V.62189), 328 $\mu$m (V.62187) (Fig. 2); perforation plates simple, hori-
zontal to slightly oblique; intervascular pitting alternate, bordered and vestured, diameter
4·5–7 $\mu$m (Figs 18, 23–25); vessel to ray and vessel to parenchyma pitting similar to inter-
vascular.

*Parenchyma.* Paratracheal: vasicentric to bluntly aliform (sheath up to 6 cells broad), some-
times confluent (Figs 11, 12); apotracheal: infrequent marginal (Fig. 5) and also banded (Figs 9,
10), associated with axial canals; rare chambered cells, composed of at least ten chambers,
probably crystalliferous (Figs 15–17).

*Rays.* Multiseriate, fusiform, commonly *en échelon* (Fig. 14); 8 per tangential mm, range
5–12; 1–4 cells wide but predominantly 2 cells wide (38–54%) (Fig. 4); height 72–504 $\mu$m (3–22
cells), mean 260 $\mu$m (11 cells, V.62188), 300 $\mu$m (13 cells, V.62187 and V.62189) (Fig. 3); sub-
homogeneous to heterogeneous III; multiseriate rays with uniseriate, marginal rows of radially
elongated cells (which are vertically taller than the non-marginal procumbent cells), or square
or upright cells (Fig. 13); uniseriate rays infrequent, composed of both procumbent and square
cells.

*Imperforate tracheary elements.* Libriform fibres, rarely locally septate; thin-walled; tangential
diameter 6–24 $\mu$m; length 500–1035 $\mu$m; pits very rare, indistinctly bordered, minute, diameter
2 $\mu$m (Figs 19, 20).

*Axial canals.* Occur in tangential series within bands of apotracheal parenchyma (Figs 8–10);
circular to oval in transverse section, tangential diameter 160 $\mu$m–300 $\mu$m, radial diameter
200 $\mu$m to 700 $\mu$m; bands of parenchyma 60 $\mu$m to 1020 $\mu$m (5–37 cells) broad.
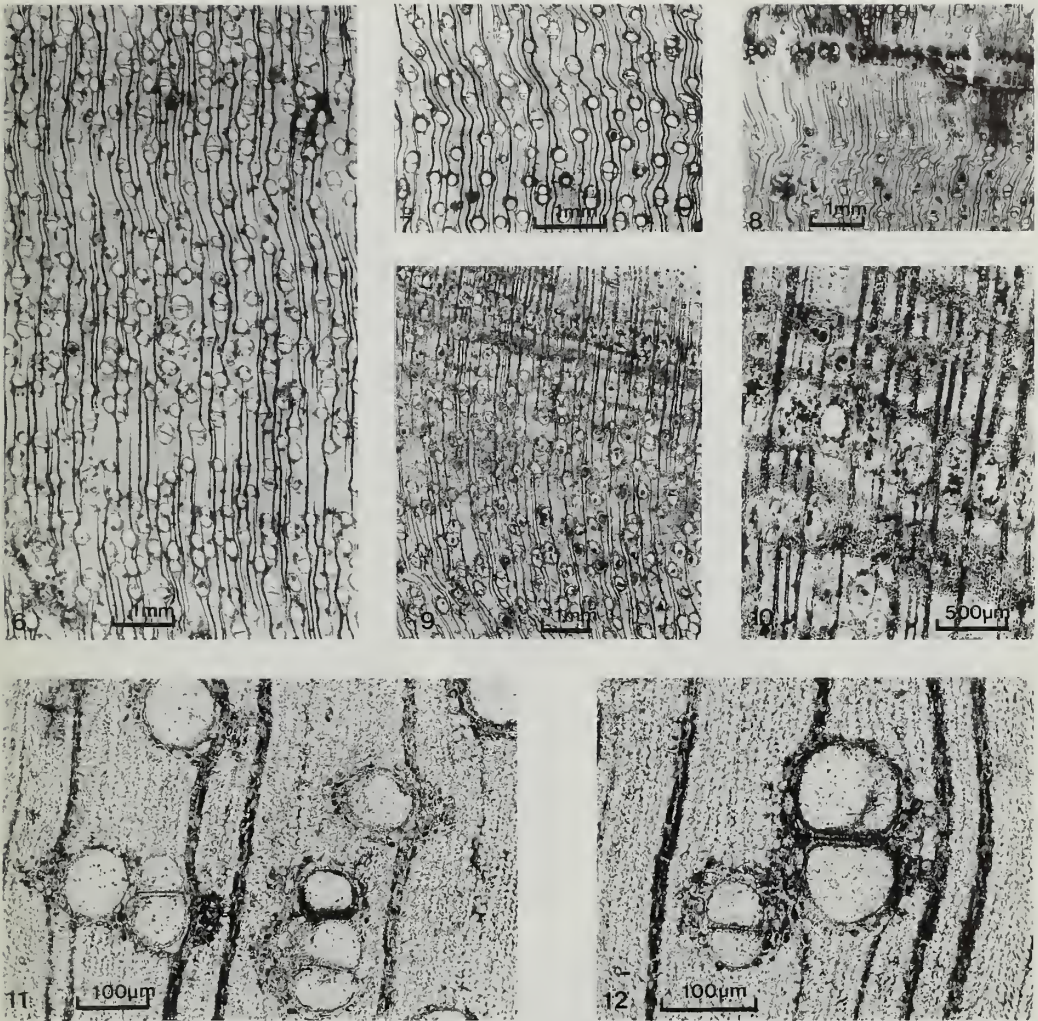
Figs 6–12  ?*Caesalpinioxylon moragjonesiae* sp. nov. Fig. 6, TS, diffuse porous vessels with vague zonation; holotype, V.62187b. Fig. 7, TS, diffuse porous arrangement of vessels; V.62188a. Fig. 8, a series of traumatic axial canals, top of figure; V.62188b. Fig. 9, traumatic axial canals with associated banded parenchyma; holotype, V.62187b. Fig. 10, detail of several canals shown in Fig. 9. Figs 11, 12, paratracheal parenchyma; V.62188a.

DISCUSSION. The three specimens are very similar in their qualitative features. Quantitatively V.62188 differs mainly in the lengths of the vessel elements, rays and fibres. Studies by Fegel (1941) have demonstrated a variation in axial element lengths between trunk, branch and root which may be the case here. Another factor in this variation may be growth trauma. The two larger specimens, V.62187–8, show series of axial canals. These were almost certainly traumatic in origin, of the gummosis type formed in response to injury (Record 1925; Barefoot & Hankins 1982). In the canal zone of V.62187 local changes are increased parenchyma, broader rays (up to five cells wide) and medium- to thick-walled fibres. In V.62188 the effect seems more widespread. It has two regions of small vessels, low vessel density and increased paratracheal parenchyma, all similar to that occurring near this specimen's axial canals.
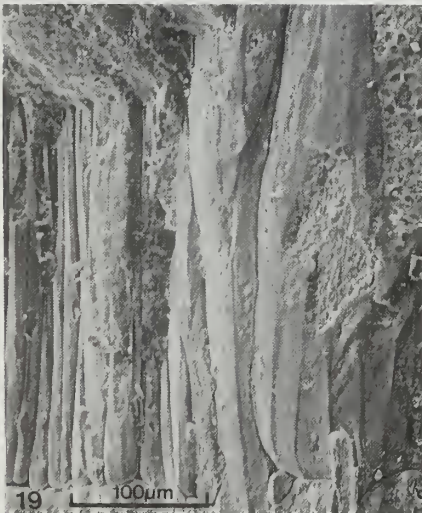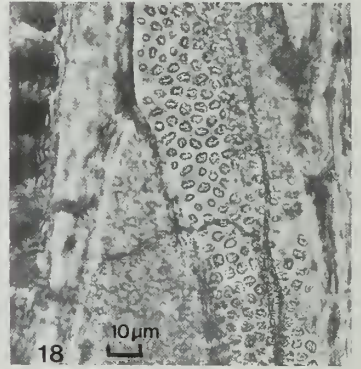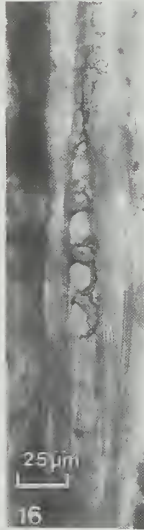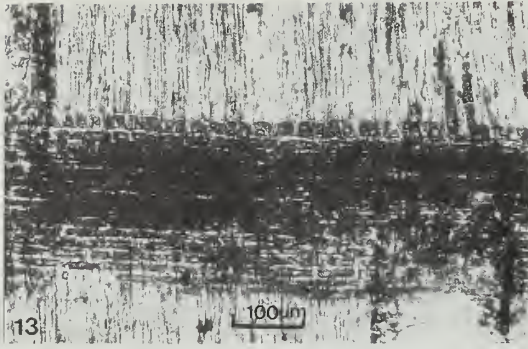
COMPARISON WITH MODERN GENERA. (All information from Metcalfe & Chalk, 1950, unless otherwise specified). The occurrence of traumatic axial canals and vestured pits is a combination found only in Combretaceae, Euphorbiaceae (Bridelieae only), Leguminosae (except in Dialiinae, Duparquetiinae, Labicheinae and all but one genus in Cercideae), Myrtaceae and Vochysiaceae (Bailey 1933; Record 1936; Quirk & Miller 1983, 1985).

Within Combretaceae the genus *Terminalia* shows many similarities to ?*C. moragjonesiae*, having wood of diffuse porous character, with multiseriate rays and paratracheal parenchyma (van Vliet 1979). Only rarely is there a slight local tendency to irregular stories of rays (Chalk *et al.* 1933). *Terminalia* and other combretaceous woods also differ in their much larger parenchyma cells, greater ratio of uniseriate to multiseriate rays, and larger pitting in the vessels.

In Euphorbiaceae vestured pits occur only in the subfamily Bridelieae. The most similar genus, *Bridelia*, differs in having scanty paratracheal parenchyma, simple vessel to ray pitting and in lacking traumatic canals.

Most genera of Myrtaceae differ from the fossil in possessing vasicentric tracheids and conspicuously bordered fibre-tracheids. The remaining genera have different vessel to ray pitting and no traumatic canals (Ingle & Dadswell 1953).

In Vochysiaceae, *Qualea* is similar to many features but like other genera in the family has simple vessel to ray pitting (Kribs 1959).

Only in Leguminosae do all the features of ?*C. moragjonesiae* occur. Of the subfamilies, the Mimosoideae differ in having entirely homogeneous rays, whilst in 75% of Papilionoideae all the elements are storied (Baretta-Kuipers 1981). The remaining Papilionoideae, which lack or only have some storied structure, and the equivalent in Caesalpinioideae (80%) can be separated by the shape of the terminal cells in the strand parenchyma (Reinders-Gouwentak & Rijsdijk 1955); this is gable-ended in the Papilionoideae but not in the Caesalpinioideae. However, this important feature is not well enough preserved in the fossils to make the distinction. Within the Caesalpinioideae and Papilionoideae traumatic axial canals are recorded in species from the following genera: *Anthonotha* (C.), *Andira* (P.), *Berlinia* (C.), *Brachystegia* (C.), *Cercidiopsis* (C.), *Cryptosepalum* (C.), *Guibourtia* (C.), *Hardwickia* (C.), *Hymenaea* (C.), *Librevillea* (C.), *Macrolobium* (C.), *Michelsonia* (C.), *Microberlinia* (C.), *Monopetalanthus* (C.), *Oddoniodendron* (C.), *Oxystigma* (C.), *Paraberlinia* (C.), *Peltogyne* (C.) and *Tetraberlinia* (C.) (Record 1936; Record & Hess 1943; Brazier & Franklin 1964; Normand & Paquis 1976; E. A. Wheeler and D. Pons, personal communication). They show the following differences when compared with the fossils. *Anthonotha, Berlinia, Brachystegia, Librevillea, Macrolobium, Michelsonia, Microberlinia, Monopetalanthus* and *Tetraberlinia* have mainly uniseriate rays. *Guibourtia, Hardwickia, Hymenaea, Peltogyne* and *Oxystigma* have much wider rays. Parenchyma is more abundant and rays are 1–2 seriate in *Oddoniodendron* and *Paraberlinia*. In *Andira* the parenchyma is banded, in *Peltogyne* markedly abaxial and in *Cryptosepalum* markedly more aliform. Material of *Cercidiopsis* was not available for study. Allowing for these differences ?*C. moragjonesiae* is most similar to species of *Tetraberlinia* and *Monopetalanthus*, but not close enough to be considered a fossil representative of either genus. However, its characters show strong affinity with Leguminosae, and most probably Caesalpinioideae.

COMPARISON WITH OTHER FOSSIL WOODS. Of the woods assigned to the fossil Leguminosae, only *Erythrophloeoxylon scholleri* (Boureau, 1957) Müller-Stoll & Mädel, 1967 and *Acacia gregorii* Gregory, 1973, exhibit traumatic axial canals. They are compared to ?*C. moragjonesiae* in Table 1, together with *Tetrapleuroxylon ersanense* (Boureau, 1953) Müller-Stoll & Mädel, 1967, the

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**Figs 13–20** ?*Caesalpinioxylon moragjonesiae* sp. nov. Fig. 13, RLS, wood ray showing a single row of square marginal cells; V.62189a. Fig. 14, TLS of wood rays; holotype, V.62187c. Fig. 15, TLS, chambered parenchyma strands amongst rays and fibres; holotype, V.62187c. Fig. 16, lower parenchyma strand from Fig. 15, showing possible crystal moulds within chambers. Fig. 17, parenchyma strand; holotype, V.62187c. Fig. 18, inter-vessel pitting; holotype, V.62187c. Fig. 19, RLS, fracture plane; some fibres on the right show pitting on the radial surface and those on the bottom left are truncated by a wood ray; holotype, V.62187n. Fig. 20, detail of fibre pitting from Fig. 19; the pits are minute and indistinctly bordered.

**Table 1** Comparison of ?*Caesalpinioxylon moragjonesiae* sp. nov. with other species of fossil Leguminosae.

| Name | ?*Caesalpinioxylon moragjonesiae* sp. nov | *Erythrophloeoxylon scholleri* (Boureau) Müller-Stoll & Mädel | *Tetrapleuroxylon ersanense* (Boureau) Müller-Stoll & Mädel | *Leguminoxylon* (?*Pahudioxylon*) *submenchikoffii* forma *sahariense* Boureau & Koeniguer | *Acacia gregorii* Gregory |
|---|---|---|---|---|---|
| Location | Republic of Mali | France | Republic of Mali | Algeria | Oregon, U.S.A. |
| Age | U. Palaeocene | Oligocene (Stampian) | post-Eocene | Eo-Oligocene | Eocene |
| **Vessels** | | | | | |
| distribution | diffuse porous | diffuse porous | semi-ring porous | diffuse porous | diffuse porous |
| "₀ solitary | 54–59 | 60 | 60 | 30–50 | mainly solitary |
| radial multiples | up to 8 | up to 4 | up to 15 | up to 4 | up to 3 |
| density | 5 per mm$^2$ | 2 per mm$^2$ | 2–4 per mm$^2$ | 3–4 per mm$^2$ | 4–11 per mm$^2$ |
| tangential diameter | 63–252 $\mu$m | 100–200 $\mu$m | 25–250 $\mu$m | 210 $\mu$m (mean) | 100–200 $\mu$m |
| length of vessel elements | 72–558 $\mu$m | 120–250 $\mu$m | 150–500 $\mu$m | 190–500 $\mu$m | 200–400 $\mu$m |
| perforation plate | simple, horizontal –oblique | simple, horizontal | simple, horizontal–oblique | simple, horizontal | simple, oblique |
| intervessel pitting | alternate, bordered, vestured, 4–5–7 $\mu$m diameter | alternate, bordered probably vestured; 4–7 $\mu$m diameter | alternate, bordered; 6–7 $\mu$m diameter | alternate, bordered, vestured; 5–6 $\mu$m diameter | |
| vessel-ray pitting | as intervessel | as intervessel | as intervessel | as intervessel | — |
| **Parenchyma** | | | | | |
| paratracheal | vasicentric to bluntly aliform, occasionally confluent | mainly confluent, abundant | aliform to confluent, abundant | bluntly aliform | vasicentric to bluntly aliform, occasionally confluent |
| apotracheal | 1) infrequent marginal 2) banded with canals | 1) regular marginal 2) ?diffuse | 1) marginal 2) diffuse | infrequent marginal | infrequent marginal |
| **Rays** | | | | | |
| seriation | (1)-2-(3)-(4) | (1)-2-(3) | (1)-2-(3) | (1)-2-(3) | (1)-(2)-(3)-4-6 |
| tangential density | 8 per mm | 6–7 per mm | 8–9 per mm | 7–8 per mm | 5 per mm |
| cellular composition | sub-homogeneous to heterogeneous III | homogeneous to heterogeneous II | heterogeneous II | homogeneous | homogeneous |
| length | 72–504 $\mu$m | 80–400 $\mu$m | up to 540 $\mu$m | 100–400 $\mu$m | 30–40 cells high |
| distribution | commonly *en échelon* | locally storied | locally storied | *en échelon* | diffuse |
| **Fibres** | | | | | |
| type | libriform, thin-walled, rarely septate | libriform, thin-walled | libriform, thin-walled | libriform, thin-walled | libriform, thick-walled |
| pitting | rare, minute bordered | probably simple | probably simple | — | — |
| axial canals | large, in apotracheal banded parenchyma | small, in apotracheal banded parenchyma | not present | not present | small, in apotracheal banded parenchyma |

**Figs 21–25** ?*Caesalpinioxylon moragjonesiae* sp. nov.; TLS fracture planes (SEM pictures). Fig. 21, pit detail destroyed by coarse recrystallization; V.62188k. Fig. 22, poorly defined structures in pit chambers; holotype, V.62187m. Fig. 23, vesture-like structures extending into the pit chamber from inside the pit aperture; part of the structure is destroyed by the kind of alteration shown in Fig. 22; V.62188k. Fig. 24, vesture-like structures proliferating within the pit chambers; holotype, V.62187m. Fig. 25, anastomosis of vesture-like structures along the plane of the pit membrane; holotype, V.62187m.

21    5 µm

22    5 µm

23    1µm

24    1 µm

25    1µm
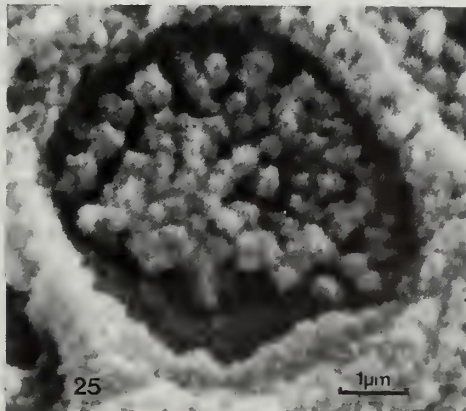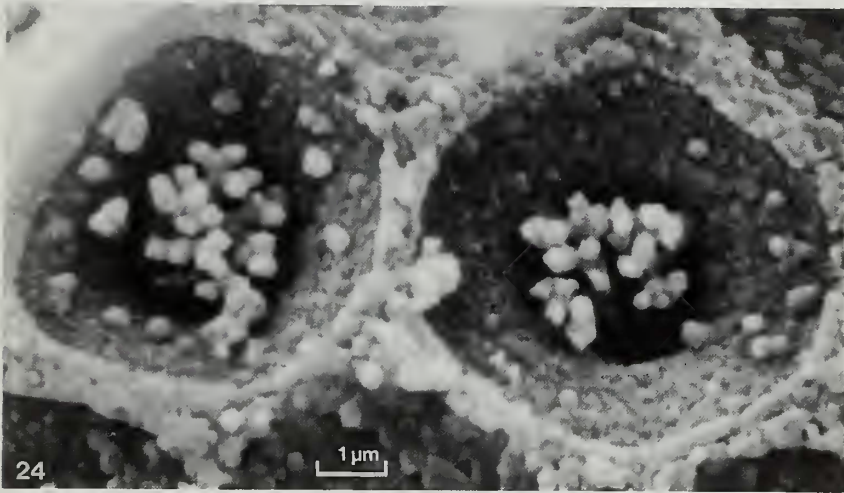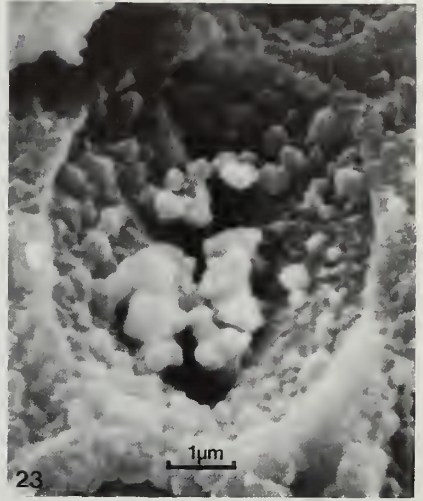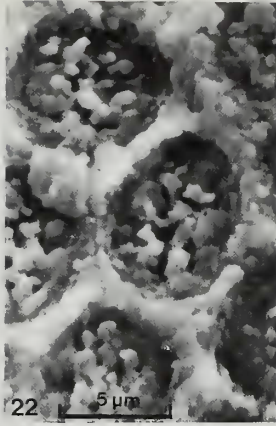
only other Leguminaceous wood from Mali, and *Leguminoxylon* (?*Pahudioxylon*) sub-
*menchikoffii* forma *sahariense* Boureau & Koeniguer, 1970. The latter species is closely compa-
rable with the new Mali wood but lacks traumatic canals. This feature appears sporadically, in
keeping with its pathological origins, and may therefore not appear in a fossil species based on
one specimen, as with *L. submenchikoffii* forma *sahariense*. In their major revision of fossil
leguminaceous wood, Müller-Stoll & Mädel (1967) anticipated the possible appearance of this
feature in twelve genera, including *Pahudioxylon menchikoffii* (Boureau, 1951), a species close to
*L. submenchikoffii* forma *sahariense*. However, as can be seen from the table, ?*C. moragjonesiae*
is distinct from the latter species in having vessels of smaller tangential diameter and a higher
proportion of solitary vessels, and in its subhomogeneous to heterogeneous III rays.

VESTURED PITS IN FOSSIL WOOD. The International Association of Wood Anatomists glossary
(1964) defines a vestured pit as 'a bordered pit with the pit cavity wholly or partially lined with
projections from the tertiary wall'. Bailey (1933), in an extensive study of pits in Recent woods,
showed that vestured pits occur in all or some of the genera within 24 dicotyledonous families.
He also described various types of vesture based on light microscopy. Scanning electron
microscopy has been used subsequently to confirm and extend Bailey's observations on Recent
woods (Meylan & Butterfield 1974; Ohtani & Ishida 1976; van Vliet 1978).
   The affinities of some fossil woods have been decided, at least in part, from light microscope
investigations of vestured pits (Louvet 1966, 1972; Koeniguer 1966, 1973; Delteil-Desneux
1972). Koeniguer mentions problems in identifying this feature and suggests the possibility of
alteration during fossilization.
   In studies of Recent wood Bailey (1933), Gale (1982) and Quirk & Miller (1985) described
structures simulating vestures ('pseudovestures'). SEM was used to establish whether pitting
was vestured or pseudovestured, where this had proved difficult to interpret using light micros-
copy. Barefoot & Hankins (1982) suggest that vestures should, therefore, be used with care for
identification. This problem is compounded when effects of fossilization are taken into account.
However, extremely clear illustrations of vestured pits in pyritized fossil wood have been
obtained recently by the use of SEM (H. P. Wilkinson, personal communication), and what I
believe to be vestured pits in silicified wood are described here for the first time, also on the
basis of SEM (Figs 23–25).
   Vessels observed on fracture surfaces of ?*C. moragjonesiae* show many areas of pitting. Often
these are either coarsely recrystallized (Fig. 21) or show structures too ill-defined to permit
critical examination (Fig. 22). In some pits or parts of pits, however, preservation is very much
better, showing structures which are closely comparable with the vestures in Recent woods. In
Fig. 23 branching structures can be seen emanating from just inside the pit aperture into the pit
chamber, towards the site of the pit membrane. These compare closely with the Recent vestures
illustrated by Gale (1982: fig. 9) and van Vliet (1978: fig. 22; 1979: pl. 2, fig. 7). In other pits the
branching has proliferated within the pit chamber (Fig. 25) in a similar fashion to those illus-
trated by Ohtani & Ishida (1976: figs 30 & 32). Anastomoses of these structures can be seen in
Fig. 24, again comparable to the Recent vestures illustrated by Ohtani & Ishida (1976: figs 29,
38, 45). These authors have shown that several types of vesture are present within the pits of
Recent woods, varying from the simplest near the pit border to more massive and complex at
or inside the pit aperture. This diversity is also shown by structures seen in Fig. 25. These fossil
structures fall well within the size maxima of Ohtani & Ishida for Recent vestures. Some
well-preserved pits in the fossil have no vesture-like structures, because, just as in Recent
woods, the vestures may be absent from some of the pits in the vessel to ray or vessel to
parenchyma pit fields (Ohtani & Ishida 1976). The fact that no similar structures could be
found within the inter-pit areas on the outer vessel walls of ?*C. moragjonesiae* again agrees with
findings based on Recent woods. Further studies of vestured pits by scanning electron micros-
copy may assist classification of fossil woods at family and subfamily level.

## Acknowledgements

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